Zonation in Marine Gastropods of Costa Rica and Species Diversity

BY

GERALD J. BAKUS

Allan Hancock Foundation, University of Southern California, Los Angeles, California 90007

During July and August of 1962 I participated in the second Advanced Science Seminar in Tropical Ecology offered at the University of Costa Rica, San Jose, Costa Rica by the University of Southern California through a grant (G-21935) from the United States National Science Foundation. One of the requirements of the program was to initiate a limited research project. A comparative study was made of littoral (intertidal) zonation of gastropod mollusks on the Pacific and Atlantic coasts of Costa Rica. The littoral zone was divided into thirds for convenience, representing high, middle and low portions.

Pacific coast zonation on rocky shores was studied at three localities: Punta Caldera near Mata de Limón, Puerto Quepos and Punta Catedral, abbreviated below as ML, PQ and PC, respectively. These regions are characterized by having a mixed tide with a daily flux of 2.6 m to 3.3 m (8 to 10 feet). Mata de Limón (within the Golfo de Nicoya) has a coastline with mangroves, considerable mud by runoff from a local river and turbid water. The site of collection and observation (Punta Caldera) was reached by boat and located about 1.5 km southwest of Caldera. The shoreline is rocky and relatively barren. Brachyuran and anomuran crabs are abundant as is one of three species of barnacles living there. The bivalve mollusk *Brachidontes puntarenensis* is especially numerous. Benthic algae are low in diversity and standing crop. Puerto Quepos and especially Punta Catedral have exposed rocky shorelines. The latter region is reminiscent of rugged portions of the coast of central and northern California but the epibiota is sparse excepting brachyuran and anomuran crabs and gastropod mollusks. Long stretches of sandy beaches are found nearby and olives (*Olivella*) are abundant there. A composite portrayal of zonation among the more conspicuous gastropods is presented as follows: The supralittoral zone is occupied by *Littorina conspersa* at Mata de Limón, found as high as 10 m above the 0-tide level. No supralittoral littorines were observed at Puerto Quepos or Punta Catedral. The high littoral zone contains *L. conspersa* (ML, PQ, PC), *L. aspera* (PQ, PC), *Nerita scabricosta ornata* (ML, PQ, PC), *Purpura patula pansa* (PQ, PC), *P. columellaris* (PQ, PC), and *Siphonaria gigas* (PQ, PC). The mid-littoral zone is characterized by *L. conspersa* (ML, PQ, PC), *L. aspera* (PQ, PC), *N. s. ornata* (ML, PQ, PC), *S. gigas* (PQ, PC), and *Fissurella virescens* (PQ, PC) with *Opeatostoma pseudodon* (PQ, PC), *Tegula pellisserpentis* (PQ, PC), *Thais melones* (PQ, PC) and *Acanthina brevidentata* (ML, PQ, PC) in the lowermost levels. The low littoral contains *O. pseudodon* (PQ, PC), *Tegula pellisserpentis* (PQ, PC), *Thais melones* (PQ, PC), *A. brevidentata* (ML, PQ, PC), *F. virescens* (PQ, PC), *Neosimnia* sp. (on a pink gorgonian near PC), *Conus nux* (PC), *Natica chemnitzii* (ML), *Polinices otis* (ML) and with *Thais biserialis* (ML) in the lowermost levels. Atlantic coast zonation on old uplifted limestone was studied at three localities: Portete, Puerto Limón, and Isla Uvita, abbreviated below as P, L, and U, respectively. These coastal areas are characterized by having a diurnal tide with a daily flux of about 1 m (3 feet). Portete, located about 5 km north of Puerto Limón, has a small bay which is rather rich in benthic algae and flowering plants. *Caulerpa, Thalassia* and the sea urchin *Diadema* are common in shallow waters. Live corals grow in pockets near the mouth of the bay. Puerto Limón has an uplifted shelf of old exposed limestone pavement pocked by numerous shallow depressions containing abundant bivalved mollusks (*Isognomon radiatus* and *Isognomon* cf. *I. bicolor*). This is especially characteristic of the shoreline north of the town. Benthic algae are diverse and relatively abundant. Numerous echinoids, ophiuroids, sea anemones, brachyuran and anomuran crabs, gastropod mollusks and several species of live corals occur in this region. Isla Uvita is located about 1 km offshore from the town of Puerto Limón. The windward side is rocky and precipitous; the crab *Grapsus grapsus* is a rapid moving and common representative there. The leeward side contains a fringing reef with a sandy lagoon between the island and the reef. Gastropod zonation, discussed below, was studied on the leeward side.

Thousands of small black snails (*Cerithium variabile*) are found on the sand in the *Thalassia* beds within the lagoon. A composite portrayal of zonation among the more conspicuous gastropods is presented as follows: The supralittoral zone contains *Tectarius muricatus* (P, L) which is found as high as 2 m above the 0-tide level. *Littorina ziczac* (P, L) occurs in the lowermost levels of this zone. The high littoral zone contains *L. ziczac* (P, L) and *L. nebulosa* (U). The mid-littoral zone is characterized by *Purpura patula* (U), *Thais haemastoma floridana* (P), *Littorina meleagris* (L), *Conus mus* (L, U), *Nerita fulgurans* (P), *N. tessellata* (P), and with *Cittarium pica* (L, U) in the lower levels. The low littoral zone contains *Cittarium pica* (L, U), *N. fulgurans* (P), *Neritina virginea* (P) and *Leucozonia nassa* (L). A list of all mollusks collected alive as well as shells is presented below in the appendix. Specimens taken are now located in the Los Angeles County Museum of Natural History under the care of Dr. James H. McLean, Curator of Invertebrate Zoology.

DISCUSSION

The supralittoral and high littoral zones on both Pacific and Atlantic coasts are dominated by Littorinidae. *Purpura, Nerita* and *Siphonaria* seemed to be missing from these zones on the Atlantic coast. It is common to find littorines predominating in the high littoral and supralittoral zones in part because of their resistance to desiccation. ROSEWATER (1963) reviewed the literature on desiccation in littorines. *Tectarius muricatus* lived for 18 months in a box. *Littorina ziczac* lived for 7 months with only infrequent wetting. Both Pacific and Atlantic coasts of Costa Rica samples contain supralittoral and littoral gastropods in which roughly half are carnivores and half herbivores. Visual observations indicated that Pacific coast stations supported about twice the standing crop of gastropods as that of the Atlantic coast but quantitative information is needed for verification. If this is a true measure of standing crop a paradox is encountered because the diversity and standing crop of benthic algae are very low along the Pacific coast; it is one of the poorest regions for benthic algae in the world (Dr. E. Yale Dawson, personal communication). Some of the reasons for differences in benthic algae along the two coasts are discussed by DAWSON (1962). However, primary production by benthic algae must be reasonably high on the Pacific coast, despite high turbidity in many areas, in order to account for the apparently greater standing crop of gastropods. It may be that benthic algae seem to be depauperate on the Pacific Coast because of high intensity grazing by invertebrates and perhaps fishes. This same phenomenon is characteristic of many other tropical regions (BAKUS, 1966a and in press).

The pioneer taxonomic work on the mollusks of Pacific Central America is that of PILSBRY & LOWE (1932). Comprehensive information on Pacific Coast mollusks is found in KEEN (1958) and on Caribbean mollusks in WARMKE & ABBOTT (1961). Recently, PAINE (1966) studied briefly the feeding relationships between two small carnivorous gastropods, a mytilid (probably *Brachidontes*) and barnacles near Mata di Limón, Costa Rica, and compared them with similar observations in the northern Gulf of California and at Mukkaw Bay, Washington. The work of PAINE (1966) and observations by the present author agree in that the local species diversity of rocky littoral and supralittoral mollusks of the Pacific Coast of Costa Rica is low. This leads to the interesting question of why does local species diversity appear to be low in Costa Rica, slightly greater in Washington and high in the northern Gulf of California. PAINE (1966) presented a logical hypothesis supported in part by field data. He stated (*op. cit.*, p. 65): "Local species diversity is directly related to the efficiency with which predators prevent the monopolization of the major environmental requisites of one species." PAINE did not consider the importance of the local substratum on the settling of larvae and spores, in order that predators have something with which to "prevent" monopolization. GIBSON (1966), from studies on foraminiferal diversity in Mississippi Sound, Gulf of Mexico, concluded that regions of high diversity are associated with stable physico-chemical environments. Both PAINE and GIBSON have contributed to ecological theory but their viewpoints are restrictive. For example, if GIBSON's hypothesis were generally true, then the rocky and sandstone intertidal region of the northern Gulf of California (where water temperatures vary between 15° C and 31° C during the year, where there is a relatively long history of runoff from the Colorado River, where a tidal flux of up to about 7 m (22 feet) occurs daily, and where the ambient air temperature may reach well over 38° C (100° F) in July-August and approach freezing (0° C) in December-January) should have a relatively low species diversity. Contrarily, the northern half of the Gulf of California contains a high diversity of littoral animals (GARTH, BELTRAN, & SAVAGE, 1960; MCLEAN, 1961; PAINE, 1966), and the Gulf of California may support the greatest diversity of shallow water invertebrates in the world (PARKER, 1964). DUSHANE & POORMAN (1967) reported over 1000 species of mollusks from Guaymas, Sonora, Mexico. Studies conducted by students and the present author on the fauna of the region of Peñasco, Sonora, Mexico (northern Gulf of California) have indicated that local species diversity of littoral invertebrates is often high.

Gibson (1966) made the generalization that in the distribution of marine benthon, species variety is lowest near shore and greatest in deeper portions of the continental shelf. However, the diversity of scleractinian corals, coral reef fishes and even temperate latitude crabs (Dr. John Garth, personal communication) is usually greatest in shallow waters. This probably holds true for many other animal groups, especially those associated with scleractinian corals. More significantly, both Gibson and Paine overlooked the very important aspect of geological history. For example, the northern Gulf of California has a unique history. It has received organisms from the Pacific Ocean by way of openings in the present Baja Peninsula (see Durham & Allison, pp. 47 - 91 *in* Garth, Beltran & Savage, 1960), it has received other organisms from the Caribbean (see Garth, Beltran & Savage, 1960 and Bakus, 1966b: 423), and several migrations of surface water isotherms have occurred along the coast of southern California and Baja California (Hubbs, 1960, 1961; Bandy, 1967). The northern Gulf of California has a complex biota consisting of elements from the cold temperate, warm temperate, subtropical and tropical regions. Moreover, it has a moderately high degree of endemism (Garth, Beltran & Savage, 1960) and curious summer and winter algal communities (Dawson, 1944: 200). Much of the Pacific coast of Costa Rica has considerably less diversity. The rocky littoral zone contains tropical forms that must resist high air temperatures and desiccation, excessive turbidity and frequent exposure to freshwater during part of the year, and probably periodic effects of upwelling. On the other hand, it is likely that the effects of predaceous, grazing and browsing fishes on the littoral biota are more pronounced in Costa Rica than in the northern Gulf of California (Bakus, 1966a).

In conclusion, more information, particularly of a quantitative nature, is needed to better understand intertidal zonation in Central America. Hypotheses that deal with species diversity in the marine environment, should be considered only as parts of an enormously complex group of variables that change with time.

ACKNOWLEDGMENT

I would like to thank the following persons: Jay M. Savage for introducing me to tropical biology; the late E. Yale Dawson for introducing me to benthic marine algae and for his companionship on field trips throughout Costa Rica; W. Jake Houk for a collection of shells from Mata de Limón, Costa Rica; James H. McLean for verifications, corrections and additions on my identifications of marine mollusks taken in Costa Rica; Manuel M. Murillo for a translation of a summary into Spanish; and James H. McLean, Los Angeles County Museum of Natural History, Jay M. Savage, Kristian Fauchald, Manuel M. Murillo, Amada Reimer, Department of Biological Sciences, University of Southern California, and Orville L. Bandy, Department of Geology, University of Southern California, for suggestions and criticisms.

APPENDIX

List of mollusks collected in Costa Rica, all of which are on deposit in the Los Angeles County Museum of Natural History

A. Pacific Coast:

1. Punta Caldera, near Caldera, Costa Rica: live mollusks, littoral and supralittoral, collected by G. Bakus, 20 July 1962.

Acanthina brevidentata (Wood, 1828)	1
Anachis sp.	7
Anachis sp.	2
Brachidontes puntarenensis (Pilsbry & Lowe, 1932)	6
Littorina conspersa Philippi, 1847	24
Natica chemnitzii Pfeiffer, 1840	2
Nerita scabricosta ornata Sowerby, 1823	1
Olivella zanoeta (Duclos, 1835)	7
Polinices otis (Broderip & Sowerby, 1829)	1
Thais biserialis (Blainville, 1832)	7
Thais triangularis (Blainville, 1832)	1
Tricolia mazatlanica (Strong, 1928)	1

2. Mata de Limón, Costa Rica: shells cast up on beach, all but one inhabited by hermit crabs, all but one collected by Jake Houk, 21 July 1962.

Acanthina brevidentata (Wood, 1828)	5
Anachis fluctuata (Sowerby, 1832)	1
Cantharus ringens (Reeve, 1846)	2
Cantharus vibex (Broderip, 1833)	1
Cassis centiquadrata (Valenciennes, 1832)	3
Cerithidea pulchra (C. B. Adams, 1852)	2
Cerithidea valida (C. B. Adams, 1852)	1
Cymatium gibbosum (Broderip, 1833)	1
Cymatium vestitum (Hinds, 1844)	1
Pitar lupanaria (Lesson, 1830), collected by G. Bakus, 20 July 1962	1
Rhinocoryne humboldti (Valenciennes, 1832)	2
Tegula byroniana (Wood, 1828)	1
Thais triangularis (Blainville, 1832)	1
Turritella sp. (juvenile)	2

3. Puerto Quepos, Costa Rica: live mollusks, littoral and supralittoral, collected by G. Bakus, 20 July 1962.

Acanthina brevidentata (Wood, 1828)	2
Littorina aspera Philippi, 1846	10
Littorina conspersa Philippi, 1847	12
Nerita scabricosta ornata Sowerby, 1823	4
Opeatostoma pseudodon (Burrow, 1815)	2
Planaxis planicostatus Sowerby, 1825	1
Purpura columellaris (Lamarck, 1822)	2
Purpura patula pansa Gould, 1853 (?1852)	2
Siphonaria gigas Sowerby, 1825	1
Tegula pellisserpentis (Wood, 1828)	3
Thais melones (Duclos, 1832)	5

4. Puerto Quepos, Costa Rica: shells cast up on beach, collected by G. Bakus, 20 July 1962.

Opeatostoma pseudodon (Burrow, 1815)	1
Purpura patula pansa Gould, 1853 (?1852)	1
Pyrene labiosa (Sowerby, 1822)	2
Siphonaria gigas Sowerby, 1825	3
Tegula panamensis (Philippi, 1849)	1
Tegula pellisserpentis (Wood, 1828)	1

5. Near Punta Catedral (1½ km south), Costa Rica, live mollusks, littoral and shallow sublittoral, collected by G. Bakus, 21 July 1962.

Conus nux Broderip, 1833	1
Fissurella virescens Sowerby, 1835	1
Neosimnia sp. (on pink gorgonian)	1

6. Near Punta Catedral (1½ km south), Costa Rica: shells cast up on beach, collected by G. Bakus, 21 July 1962.

Conus purpurascens Sowerby, 1833	4
Cypraea arabicula Lamarck, 1811	2
Cypraea cervinetta Kiener, 1843	3
Cypraea robertsi Hidalgo, 1906	1
Fissurella virescens Sowerby, 1835	2
Oliva spicata (Röding, 1798)	5
Strombus peruvianus Swainson, 1823	1
Trigoniocardia guanacastensis (Hertlein & Strong, 1947) valves only	3

B. Atlantic Coast:

7. Portete, Costa Rica: live mollusks, littoral and supralittoral, collected by G. Bakus, 4 August 1962.

Anadara ovalis (Bruguière, 1789)	1
Isognomon radiatus (Anton, 1839)	1
Leucozonia nassa (Gmelin, 1791)	3
Littorina nebulosa (Lamarck, 1822)	11
Littorina ziczac (Gmelin, 1791)	1
Nerita fulgurans Gmelin, 1791	3
Nerita tessellata Gmelin, 1791	1
Neritina virginea (Linnaeus, 1758)	15
Tectarius muricatus (Linnaeus, 1758)	3
Thais haemastoma floridana (Conrad, 1837)	4

8. Portete, Costa Rica: shells cast up on beach, collected by G. Bakus, 4 August 1962.

Charonia variegata (Lamarck, 1816)	1
Cittarium pica (Linnaeus, 1758)	1
Columbella mercatoria (Linnaeus, 1758)	1
Cypraea spurca acicularis Gmelin, 1791	1
Strombus raninus Gmelin, 1791	1

9. Puerto Limón, Costa Rica: live mollusks, littoral and supralittoral, collected by G. Bakus, 7 July 1962.

Cittarium pica (Linnaeus, 1758)	1
Conus mus Hwass, 1792	1
Isognomon cf. *I. bicolor* (C. B. Adams, 1845)	3
Isognomon radiatus (Anton, 1839)	1
Leucozonia nassa (Gmelin, 1791)	1
Littorina meleagris (Potiez & Michaud, 1838)	2
Littorina ziczac (Gmelin, 1791)	1
Modulus modulus (Linnaeus, 1758)	1
Tectarius muricatus (Linnaeus, 1758)	1
Vasum muricatum (Born, 1778)	1

10. Puerto Limón, Costa Rica: shells cast up on beach, collected by G. Bakus, 7 July 1962.

Arcopagia fausta (Pulteney, 1799)	1
Cerithium eburneum Bruguière, 1792	1
Columbella mercatoria (Linnaeus, 1758)	1
Conus mus Hwass, 1792	1
Crassispira sp.	1
Isognomon sp.	1
Littorina ziczac (Gmelin, 1791)	1
Nerita fulgurans Gmelin, 1791	4
Nerita tessellata Gmelin, 1791	2
Tectarius muricatus (Linnaeus, 1758)	1

11. Puerto Limón, Costa Rica: mollusks in shallow sublittoral, collected by G. Bakus, 8 July 1962.

Vasum muricatum (Born, 1778)	2

12. Isla Uvita, Costa Rica: live mollusks, littoral and supralittoral, collected by G. Bakus, 8 July 1962.

Cerithium litteratum (Born, 1778)	2
Cerithium variabile C. B. Adams, 1852	2

Cittarium pica (Linnaeus, 1758)	1
Codakia orbicularis (Linnaeus, 1758)	1
Conus mus Hwass, 1792	1
Leucozonia nassa (Gmelin, 1791)	1
Littorina nebulosa (Lamarck, 1822)	4
Purpura patula (Linnaeus, 1758)	1

13. Isla Uvita, Costa Rica: shells cast up on beach, collected by G. Bakus, 8 July 1962.

Cittarium pica (Linnaeus, 1758)	2
Conus mus Hwass, 1792	2
Cymatium pileare (Linnaeus, 1758)	1
Littorina nebulosa (Lamarck, 1822)	2

LITERATURE CITED

Bakus, Gerald J.

1966 a. Some relationships of fishes to benthic organisms on coral reefs. Nature 210 (5033): 280 - 284

1966 b. Marine poecilosceridan sponges of the San Juan Archipelago, Washington. Journ. Zool. London 149: 415 - 531

(in press) The feeding habits of fishes and primary production at Eniwetok, Marshall Islands. Micronesica

Bandy, Orville L.

1967. Problems of Tertiary foraminiferal and radiolarian zonation, circum-Pacific area. pp. 95 - 102 *in*: Hatai, K. (ed.) Tertiary correlations and climatic changes in the Pacific. Symp. No. 25 of the 11th Pacific Sci. Congr. (1966). Sasaki Publ. Co., Sendai, Japan, pp. 1 - 102

Dawson, E. Yale

1944. The marine algae of the Gulf of California. Allan Hancock Pacif. Exped. 8 (10): 1 - 452

1962. Additions to the marine flora of Costa Rica and Nicaragua. Pacif. Nat. 3 (13): 375 - 395

DuShane, Helen & Roy Poorman

1967. A checklist of mollusks for Guaymas, Sonora, Mexico. The Veliger 9 (4): 413 - 441; 1 map (1 April 1967)

Garth, J. S., E. Beltran & Jay M. Savage (Chairmen)

1960. Symposium: The biogeography of Baja California and adjacent seas. Syst. Zool. 9 (2 - 4): 47 - 91, 93 - 231

Gibson, L. B.

1966. Some unifying characteristics of species diversity. Contrib. Cushman Found. Foram. Res. **17** (4): 117 - 124

Hubbs, Carl

1960. Quaternary paleoclimatology of the Pacific coast of North America, pp. 105 - 112 *in*: O. E. Sette & J. D. Isaacs (eds.), Part 2. Symposium on the changing Pacific Ocean in 1957 and 1958. Invest. Reprt. Calif. Co-op. Ocean Fish. **7**: 13 - 217

1961. Some highlights from the natural radiocarbon datings of La Jolla laboratory. Science, N. Y. **134**: 1430

Keen, A. Myra

1958. Sea shells of tropical West America; marine mollusks from Lower California to Colombia. i - xi + 624 pp.; illus. Stanford, Calif. (Stanford Univ. Press)

McLean, James H.

1961. Marine mollusks from Los Angeles Bay, Gulf of California. Trans. San Diego Soc. Nat. Hist. 12 (28): 449 - 476

Paine, Robert T.

1966. Food web complexity and species diversity. Amer. Natur. 100 (910): 65 - 75

Parker, Robert H.

1964. Zoogeography and ecology of some macro-invertebrates, particularly molluscs, in the Gulf of California and the continental slope off Mexico. Vidensk. Medd. Dansk naturh. Foren. 126: 1 - 178

Pilsbry, Henry Augustus & Herbert N. Lowe

1932. West Mexican and Central American mollusks collected by H. N. Lowe, 1929 - 31. Proc. Acad. Nat. Sci. Philadelphia 84: 33 - 144; 7 figs.; plts. 1 - 17; 2 photogr. (21 May 1932)

Rosewater, Joseph

1963. Resistance to desiccation in dormancy by *Tectarius muricatus*. The Nautilus 76 (3): 111

Warmke, Germaine L. & Robert Tucker Abbott

1961. Caribbean seashells; a guide to the marine mollusks of Puerto Rico and other West Indian islands, Bermuda and the lower Florida Keys. x + 346 pp.; 44 plts.; 34 text figs.